On Changes in the Glomeruli and Tubules of the Kidney accompanying Activity.

By T. G. Brodie, M.D., F.R.S., and J. J. Mackenzie, M.B.

(Received December 9, 1912,—Read February 20, 1913.)

(From the Physiological and Pathological Laboratories of the University of Toronto.)

[Plate 27.]

The experiments described in this paper were designed to test the correctness of the view put forward by one of us,* namely, that the glomerulus is a propulsor. If this view be correct, the marked dilatation of the tubules, which is so prominent a feature in a kidney after active diuresis, is simply the expression of the forcible distension of the tubule from within, effected by the discharge of fluid from the glomerulus down the tubule, the active propelling and dilating force being the intraglomerular blood-pressure transmitted through the glomerular capillary cells and epithelium. As, however, the condition of the glomerulus after active secretion has not been made the subject of extensive observation, it seemed probable that a thorough study of the alterations in size and appearance of both tubule and glomerulus might give many points of importance in criticising the propulsion theory. Thus, if the capsule be free to expand, we may find it enlarged after active diuresis; and again, if the propulsive action of the glomerulus is complete and instantaneous, we should find the glomerulus filling Bowman's capsule completely under all conditions. But it was also possible that, after a very free secretion of water, there might be a considerable accumulation of fluid between the glomerulus and the capsule wall. We therefore measured the sizes of the capsules, the glomeruli and the tubules in kidneys, before and after diuresis had been set up under varying conditions. The more important of these states were:—

1. The kidney at rest.
2. The kidney secreting freely. This we term an "active free" kidney.
3. Decapsulated and secreting freely. This we term an "active decapsulated" kidney. The aim of the procedure was to test the explanation offered by the theory as to the meaning of the Capsule.†

* *Vide* Croonian Lecture, *supra*.

† As in the course of this paper we shall be referring constantly to the Capsule of the kidney and to Bowman's capsule, we will, in order to avoid needless repetition, distinguish between them by employing a capital letter whenever we refer to the former.

4. With the ureter ligatured. This we term an "active obstructed" kidney.

We soon found that the different parts of the renal tubule, and more especially of Bowman's capsule and the glomerulus, varied considerably in size in different animals, so that it is necessary in making comparisons to use only, in the first instance, opposite kidneys in the same animal. Hence, our series of experiments comprises each possible combination in the above-named types of experiments.

All our experiments were performed upon cats anæsthetised with a mixture of chloroform and ether.

In all experiments, the kidney was removed and fixed in the following way. It was first carefully freed from subperitoneal fat, and a ligature then tied tightly around the pedicle close to the hilum. A second ligature was next tied around the pedicle a little nearer the aorta, and the pedicle divided between the ligatures. The object of ligaturing the pedicle was to keep the urine within the tubules, and as far as possible in the position it occupied at the instant of ligature. The kidney was dropped intact into a beaker of 20-per-cent. formalin made up with 0·9 per cent. NaCl. The beaker and solution had previously been weighed, and it was now weighed a second time, giving the weight of the kidney. At the end of an hour, the kidney was sliced into thin sections, fixation in formalin completed, and the pieces imbedded and sections prepared. The following measurements were then taken:—

1. An equatorial diameter of the capsule at right angles to the polar diameter.

2. The polar diameter, *i.e.* one passing through the point of entrance of the blood-vessels.

3. The greatest distance between the glomerulus and the capsule if the two were not in contact.

4. The maximal diameter of a typical proximal convoluted tubule.

5. The diameter of its lumen.

6 and 7. Similar measurements of a typical section of the distal convoluted tubule.

The glomeruli measured were taken at random, care being exercised only to measure those in which the section passed centrally. This was generally fairly easy to attain by taking those which showed the point of entrance of the blood-vessel into the glomerulus. From these measurements, calculations were made of the approximate volumes of the capsule and the glomerulus respectively. To obtain these, we regarded the capsule as equal in volume

to a sphere whose diameter was the mean of the two diameters of the capsule. The figures representing volumes given in this paper were obtained by cubing the mean radius of the capsule expressed in microns, and dividing it by 1000. Hence, to convert the figures into cubic millimetres, they must be multiplied by $4{\cdot}2 \times 10^{-6}$. The glomerulus was also compared to a sphere, whose diameter was the diameter of the capsule minus the maximum space between the glomerular surface and the capsular surface. The difference between the two volumes thus ascertained gives us an approximate estimate of the volume of the fluid contained within the capsule.

In measuring the tubules a section of a proximal convoluted tubule lying near to the glomerulus was selected, and that section of the distal convoluted tubule which lies close to the point of entrance of the vessels into the glomerulus. Hence the proximal tubule probably belonged to the glomerulus measured, and the distal tubule certainly did so belong.

I. *Comparison between a Resting and an Active Kidney.*

A. *The Glomerulus and Capsule.*—There are always marked differences between a resting and an active glomerulus. A resting glomerulus appears to be made up of a dense tissue closely packed with nuclei (fig. 1). The glomerular surface always lies in contact with the capsule wall, and the whole structure is usually irregularly quadrangular in outline. After activity the glomerulus stands away clearly from the capsule. The outline of the glomerulus is lobular, and in structure it is much looser than the resting glomerulus (fig. 2). It also appears to be filled with large vacuole-like spaces approximately circular in section. The nuclei are well separated. As a rule the number of blood corpuscles contained in the glomerular vessels is quite small, far fewer than in the resting glomerulus. This we think may be due to the expulsion of the blood from the capillary loops after excision of the kidney, or to *post-mortem* laking of the corpuscles. The latter may be produced by the diffusion of water from the capsule through the walls of the capillary loops after the epithelial cells have died, and before the fixative has had time to act upon them. This would account for the very characteristic vacuolated appearance of the glomeruli already alluded to.

We were never able to keep the blood in a kidney that was excised at the height of activity. At the instant of excision such a kidney is hard and tense, and instantly becomes soft when the first ligature is tied round the pedicle. This is even the case though the vein be first ligatured, and though the kidney may have been separated from its surrounding tissues before the diuretic was administered in order to give ample time for closure of the

many small vessels passing through the Capsule. Even then there is a distinct escape of blood through the Capsule, and the cortex rapidly pales in colour as the tension falls. The greater the tension at the instant of ligature, the greater is this paling of the cortex, and the sections of such kidneys may show but traces of blood in any of the capillaries, and but little in the veins.

The change in the shape of Bowman's capsule when the kidney becomes active is very distinctive. It becomes circular or elliptic in section, and there is always fluid between the glomerulus and the capsule wall. In many instances we have noted one other highly suggestive appearance. This is that the first portion of the proximal tubule has, in cases in which a free diuresis was established, been distended so as to appear almost a part of the capsule wall. An instance of this is illustrated in fig. 3. It is a very clear indication that the capsule and the first part of the convoluted tubule have been subjected to a high internal pressure. There are further indications, moreover, that the capsule has been distended to a size much larger than it appears in the section after fixation. The action of a high intra-capsular pressure also adequately explains the change of shape from irregularly quadrangular to spheroidal or ellipsoidal.

B. *The Tubules.*—The contrast between the tubules at rest and after they have been in activity is just as striking, and in some particulars has already been described by several observers. In this paper we deal entirely with changes in the total diameter and in the lumen of the tubules, and, moreover, restrict our attention for the most part to the two convoluted tubules.

The magnitude of these several changes is brought out by the following measurements taken from Experiment 10. The measurements are in microns, and each is the mean of 10 measurements:—

Expt. 10.—R. kidney resting. L. kidney free.

	R. μ.	L. μ.
Glomeruli and capsules—		
Equatorial diameter	108·4	144·0
Polar diameter	78·4	103·6
Space	3·0	23·8
Hence		
Mean diameter capsule	93·4	123·8
„ „ glomerulus	90·4	100·0
Approximate volume capsule ...	102	237
„ „ glomerulus	92	125
„ „ fluid.....	10	112

Convoluted tubules—			
Proximal.	External diameter ...	41·4	41·4
	Lumen	0·0	17·6
Distal.	External diameter ...	21·2	32·4
	Lumen	7·2	20·6

	grm.
Weight of R. kidney	10·9
„ L. kidney	16·2

These figures show most clearly how extensive a change in size of the different parts of the renal tubule occurs when it is thrown into activity. Thus the capacity of the capsule is more than doubled (to 232 per cent.), chiefly because of the very large accumulation of fluid which has been secreted. The glomerulus is, however, increased to 136 per cent. of the volume of the glomerulus at rest. The differences are in reality still more marked, for a glomerulus actually at rest has no space between the glomerulus and the capsule wall, whereas in the right kidney of this animal no less than 7 of the 10 capsules measured contained fluid, though but small in amount.

We may conclude, then, that both Bowman's capsule and the glomerulus are distensible structures, and, further, that during activity the glomerulus does not remain in contact with the capsule wall, all of which strongly opposes the filtration theory of glomerular activity. These two conclusions are confirmed by every experiment we have performed.

When we turn to the measurements of the tubules the changes are equally striking. The external diameter of the proximal tubule is usually unaltered, but, whereas the resting tubule has no lumen, the tubule after action has a large lumen (43 per cent. of the total diameter). With the distal convoluted tubule the case is somewhat different. The total diameter is markedly increased (to 153 per cent.). The lumen of the resting tubule is 34 per cent., but that of the active tubule 64 per cent. of the total diameter of the tubule. Also, the lumen of the active tubule is 2·86 times greater than that of the resting. Apparently, then, the basement membrane of the proximal convoluted tubule is practically inextensible with the forces at play in this instance, whereas that of the distal convoluted tubule is extensible. In both tubules the cells are distinctly flattened against the basement membrane as a result of activity.

II. *Comparison between a Resting and a Decapsulated Kidney.*

The measurements obtained in an experiment of this character (Experiment 11) were as follows:—

Expt. 11.—R. kidney, resting. L. kidney, decapsulated and secreting freely.

		R. μ.	L. μ.
Glomeruli and capsules—			
	Equatorial diameter	100·4	112·0
	Polar diameter	73·6	95·2
	Space	3·0	14·6
Hence			
	Mean diameter capsule	87·0	103·6
	„ „ glomerulus	84·0	89·0
	Approximate volume capsule.....	82	139
	„ „ glomerulus	74	88
	„ „ fluid	8	51
Convoluted tubules—			
Proximal.	External diameter ...	46·0	42·0
	Lumen.....	1·4	19·4
Distal.	External diameter ...	24·0	28·0
	Lumen	10·8	17·6

	grm.
Weight of R. kidney	8·4
„ L. kidney	10·6

In this experiment the changes are entirely in the same direction as in the preceding, and the magnitude of the various changes is also approximately the same. If anything, the free kidney in the preceding experiment showed rather greater changes in comparison to the resting than did the decapsulated kidney of this experiment. The difference is, however, accounted for by the fact that the diuresis in Experiment 10 was greater than in Experiment 11.

The increase in volume of the capsule is to 170 per cent., of the glomerulus to 119 per cent. One notable difference is that in this experiment the external diameter of the proximal convoluted tubule was less after diuresis than when at rest.

III. *Comparison of a Free Kidney with a Free Decapsulated Kidney.*

Expt. 3.—R. kidney free. L. kidney free and decapsulated.

	R. μ.	L. μ.
Glomeruli and capsules—		
Equatorial diameter	135·2	142·4
Polar diameter	100·8	112·0
Space	15·2	20·6

Hence

Mean diameter capsule		118·0	127·1
„ „ glomerulus		100·8	106·5
Approximate volume capsule.....		205	257
„ „ glomerulus		128	151
„ „ fluid.....		77	106
Convoluted tubules—			
Proximal.	External diameter ...	44·8	48·0
	Lumen.....	13·0	19·8
Distal.	External diameter ...	33·2	39·2
	Lumen.....	24·8	29·2

	grm.
Weight of R. kidney.....	20·6
„ L. kidney.....	19·1

The two kidneys show the general changes of a diuresis in a well-marked manner. The experiment further shows that the effect of decapsulation is to cause a relatively greater expansion of both capsule and glomerulus. Also, the capsule is not so well emptied as in the normally active kidney. The difference in the dilatation of the convoluted tubules is again in favour of the decapsulated kidney. This is particularly seen with regard to the lumen of the proximal convoluted tubule. Whereas the ratio of the external diameter of the first convoluted tubule of the decapsulated kidney to that of the free kidney is 1 to 1·07, the ratio of the lumina is 1 to 1·53.

Hence we may conclude that decapsulation results in an increased distension of all the cortical parts of the kidney tubule when it is thrown into activity.

In the next group of experiments one of the kidneys was obstructed. The group comprises three comparisons.

IV. *Comparison of a Resting Kidney with an Obstructed Kidney.*

Expt. 12.—R. kidney resting. L. kidney obstructed.

	R. μ.	L. μ.
Glomeruli and capsules—		
Equatorial diameter	98·4	130·4
Polar diameter	76·0	111·2
Space	1·2	24·8

Hence

Mean diameter capsule	87·2	120·8
„ „ glomerulus	86·0	96·0
Approximate volume capsule.....	83	220
„ „ glomerulus	80	111
„ „ fluid.....	3	109

Convoluted tubules—

Proximal.	External diameter ...	44·0	42·8
	Lumen.....	0·0	19·4
Distal.	External diameter ...	25·4	31·8
	Lumen.....	11·0	21·8

	grm.
Weight of R. kidney	7·7
„ L. kidney	10·9

The general changes are in the same direction as before. Perhaps the most marked difference between this and the previous kidneys examined is the large volume of fluid contained within the capsule, and the relatively small size of the glomerulus. Again, we note that there is no change in the external diameter of the proximal convoluted tubule, whereas the distal is extended to 125 per cent. of its resting diameter. As illustrated by the lumina, a very considerable volume of urine is collected within the tubules, particularly in the distal tubule.

V. *Comparison of a Free Kidney with an Obstructed Kidney.*

Expt. 6.—L. kidney free. R. kidney obstructed.

	R. μ.	L. μ.
Glomeruli and capsules—		
Equatorial diameter	99·6	110·8
Polar diameter	77·2	100·0
Space	6·2	16·0

Hence

Mean diameter capsule	88·4	105·4
„ „ glomerulus	82·2	89·4
Approximate volume capsule.....	86	146
„ „ glomerulus	69	89
„ „ fluid	17	57

Convoluted tubules—			
Proximal.	External diameter ...	39·2	39·4
	Lumen	6·6	14·0
Distal.	External diameter ...	22·8	28·2
	Lumen	12·6	18·4

	grm.
Weight of L. kidney	13·5
„ R. kidney	15·5

This experiment shows quite clearly the great effect of obstruction upon the distension of the capsule and accumulation of fluid within the capsule. Obstruction also causes a distinct further dilatation of the distal convoluted tubule, and an increase in the lumina of both parts of the tubule.

VI. *Comparison of a Free Decapsulated Kidney with an Obstructed Kidney.*

Expt. 7.—R. kidney decapsulated. L. kidney obstructed.

		R. μ.	L. μ.
Glomeruli and capsules—			
Equatorial diameter		121·2	130·4
Polar diameter		102·0	111·2
Space		9·8	20·0
Hence			
Mean diameter capsule		111·6	120·8
„ „ glomerulus		101·8	100·8
Approximate volume capsule ...		174	220
„ „ glomerulus		132	128
„ „ fluid		42	92
Convoluted tubules—			
Proximal.	External diameter ...	42·0	41·4
	Lumen	15·4	17·6
Distal.	External diameter ...	28·6	31·0
	Lumen	20·4	21·2

	grm.
Weight of R. kidney	10·7
„ L. kidney	11·0

The results of the measurements in this experiment show that obstruction of the ureter results in an increased expansion of the capsule of the obstructed, as compared to that of the free active kidney; this is entirely due to a greater accumulation of fluid within it. The convoluted tubules

show corresponding differences. The effect as before is mainly felt in the distal tubule, which shows a somewhat greater expansion. The lumina in the proximal tubules are greater in the obstructed kidney than in the free kidney. In this experiment the blood-pressure was rather low, but the diuresis good.

In all these obstructed kidneys the effect upon the medulla is very marked. Not only is the pelvis of the kidney greatly distended, but the pyramid is driven back towards the cortex, and appears very much shrunken. We have often seen it so contracted as to appear only about a quarter or less of its normal size. In the sections the collecting tubules are flattened and empty, the loops of Henle, however, contain fluid, and often appear to be about the same size as in the normal active kidney. The appearance of the pyramids is so characteristic that one can at once decide whether or no the ureter of that kidney had been obstructed in the experiment.

The last group of experiments comprises a comparison of various kidneys with a kidney which was both obstructed and decapsulated.

VII. *Comparison of a Resting Kidney with a Decapsulated and Obstructed Kidney.*

Expt. 13.—R. kidney resting. L. kidney decapsulated and obstructed.

	R. μ.	L. μ.
Glomeruli and capsules—		
Equatorial diameter	110·4	128·0
Polar diameter	79·6	110·8
Space	3·4	21·2
Hence		
Mean diameter capsule	95·0	119·4
„ „ glomerulus.....	91·6	98·2
Approximate volume capsule.....	107	213
„ „ glomerulus	96	118
„ „ fluid.....	11	95
Convoluted tubules—		
Proximal. External diameter ...	46·0	49·6
Lumen.....	0·0	26·4
Distal. External diameter ...	21·8	34·4
Lumen.....	10·6	24·4

	grm.
Weight of R. kidney	14·5
„ L. kidney	19·3

An examination of the figures brings out an enormous increase in the size of the capsules, due chiefly to the increase in the amount of the fluid contained. The effect upon the convoluted tubules is again most marked. Otherwise the figures require no further comment.

The right kidney was not completely at rest, as was indicated by the microscopic appearance of the glomeruli. In every instance there was fluid between the glomerulus and the capsule.

VIII. *Comparison of a Free Kidney with a Decapsulated and Obstructed Kidney.*

Expt. 1.—R. kidney free. L. kidney decapsulated and obstructed.

	R. μ.	L. μ.
Glomeruli and capsules—		
Equatorial diameter	135·6	143·6
Polar diameter	106·8	125·6
Space	23·8	31·6
Hence		
Mean diameter capsule	121·2	134·6
„ „ glomerulus.....	97·4	103·0
Approximate volume capsule.....	223	305
„ „ glomerulus	116	137
„ „ fluid	107	168
Convoluted tubules—		
Proximal. External diameter ...	48·2	51·4
Lumen.....	13·2	24·0
Distal. External diameter ...	38·6	39·8
Lumen.....	29·0	30·8

The general result of the experiment shows that the glomeruli and convoluted tubules are more distended in the decapsulated and obstructed kidney than in the free kidney. In this instance the volume of the capsules became enormous, with only a slight increase in the volume of the glomeruli. We would emphasise the very great size of the lumen of the proximal convoluted tubule.

Expt. 4.—R. kidney free. L. kidney decapsulated and obstructed.

	R. μ.	L. μ.
Glomeruli and capsules—		
Equatorial diameter	137·6	152·4
Polar diameter	112·4	122·4
Space	10·4	22·0

Hence

Mean diameter capsule		125·0	137·4
„ „ glomerulus.....		114·6	115·4
Approximate volume capsule ...		244	324
„ „ glomerulus		188	192
„ „ fluid.....		56	132
Convoluted tubules—			
Proximal.	External diameter ...	45·6	43·4
	Lumen	15·2	22·8
Distal.	External diameter ...	27·8	29·4
	Lumen	15·8	21·2

	grm.
Weight of R. kidney.....	16·5
„ L. kidney	18·7

The results obtained in this experiment in every way confirm those shown in the previous experiment.

IX. *Comparison of a Decapsulated Kidney with a Decapsulated and Obstructed Kidney.*

Expt. 2.—L. kidney decapsulated. R. kidney decapsulated and obstructed.

		L. μ.	R. μ.
Glomeruli and capsules—			
Equatorial diameter		142·4	161·2
Polar diameter		122·4	129·2
Space		6·2	12·4

Hence

Mean diameter capsule		132·4	145·2
„ „ glomerulus.....		126·2	132·8
Approximate volume capsule ...		290	383
„ „ glomerulus		251	293
„ „ fluid.....		39	90
Convoluted tubules—			
Proximal.	External diameter ...	47·4	47·2
	Lumen	12·4	19·2
Distal.	External diameter ...	30·4	36·4
	Lumen	18·8	24·2

	grm.
Weight of L. kidney	13·6
„ R. kidney.....	16·6

The results of the experiment are again very decisive, a notable point being the large volume of the glomeruli in both kidneys. We would again point out that the main effect upon the convoluted tubules is seen in the distal tubules.

Expt. 5.—R. kidney decapsulated. L. kidney decapsulated and obstructed.

	R. μ.	L. μ.
Glomeruli and capsules—		
Equatorial diameter	144·8	151·6
Polar diameter	111·6	136·8
Space	24·0	37·6
Hence		
Mean diameter capsule	128·2	144·2
„ „ glomerulus.....	104·2	106·6
Approximate volume capsule ...	263	375
„ „ glomerulus	141	151
„ „ fluid	122	224
Convoluted tubules—		
Proximal. External diameter ...	45·6	51·0
Lumen.....	20·8	25·2
Distal. External diameter ...	34·0	42·0
Lumen	23·0	30·6

	grm.
Weight of R. kidney.....	17·6
„ L. kidney	18·0

The figures are in agreement with those of the preceding experiment, with the exception that the volume of the glomeruli in this instance is small. In Experiment 2 the blood-pressure was low (83 mm. Hg) and the diuresis moderate, while in Experiment 5 the blood-pressure was high (130 mm. Hg) and the flow of urine rapid.

X. *Comparison of an Obstructed Kidney with a Decapsulated and Obstructed Kidney.*

Expt. 8.—L. kidney obstructed. R. kidney decapsulated and obstructed.

	L. μ.	R. μ.
Glomeruli and capsules—		
Equatorial diameter	109·2	108·0
Polar diameter	95·6	95·2
Space	11·8	9·2

Hence

Mean diameter capsule		102·4	101·6
„ „ glomerulus		90·6	92·4
Approximate volume capsule ...		134	131
„ „ glomerulus		93	99
„ „ fluid.....		41	32
Convoluted tubules—			
Proximal.	External diameter ...	40·4	41·4
	Lumen.....	17·8	18·2
Distal.	External diameter ...	25·4	29·6
	Lumen.....	17·2	21·0

	grm.
Weight of R. kidney	15·8
„ L. kidney	15·8

In this experiment the blood-pressure was low and the flow of urine small, and with it again the volume of fluid in the capsule is small. In general, it confirms the result of the preceding experiments. Decapsulation combined with obstruction produces a greater distension of the tubules than obstruction alone. With a more abundant diuresis than occurred in this experiment a similar result is found in the capsules and glomeruli.

In the following tables we collect the results obtained in our thirteen experiments. In the first we give the means of the approximate volumes of Bowman's capsule, glomerulus and fluid, and in the second the ratios of these to the similar structures in the resting kidney.

We would not lay much stress upon comparisons between these figures, except when the differences are very marked. There are so many varying factors upon which the actual magnitudes of the measurements depend that to do so would lead to erroneous conclusions. Thus, the results vary with the blood-pressure, with the degree of diuresis established, the duration of the diuresis, and especially with the degree of extensibility of the kidney Capsule, and of the general renal tissues, both of which we know to vary greatly in different animals. Table II, however, shows very decisively the enormous changes in size of the glomerulus and capsule caused by active secretion of water, and more especially in the very great accumulation of water within the capsule during activity. All these results are of the highest importance in disproving the possibility of filtration at the glomerular surface.

Table I.

	Volume Bowman's capsule.	Volume glomerulus.	Volume fluid.	No. of experiments.
Resting	94	85	9	4
Active free	227	137	90	4
„ decapsulated	229	162	67	5
„ obstructed	196	136	60	3
„ decapsulated and obstructed	277	157	120	6

Table II.—Ratios.

	Bowman's capsule.	Glomerulus.	Fluid.
Resting	1·00	1·00	1·00
Active free	2·42	1·61	10·00
„ decapsulated	2·44	1·91	7·44
„ obstructed	2·09	1·60	6·67
„ decapsulated and obstructed	2·95	1·85	13·34

In Tables III and IV we give similar figures for the convoluted tubules.

Table III.

	Proximal.		Distal.	
	External diameter.	Lumen.	External diameter.	Lumen.
Resting	44·4	0·4	23·4	9·9
Active free	45·0	14·8	33·0	22·6
„ decapsulated	46·0	17·3	33·2	22·2
„ obstructed	42·0	19·0	29·3	20·3
„ decapsulated and obstructed	47·3	22·6	35·3	25·4

Table IV.—Ratios.

	Proximal.		Distal.	
	External diameter.	Lumen.	External diameter.	Lumen.
Resting	1·00	1·00	1·00	1·00
Active free	1·01	37·00	1·41	2·28
„ decapsulated	1·04	43·25	1·42	2·24
„ obstructed	0·95	47·50	1·25	2·05
„ decapsulated and obstructed	1·07	56·50	1·51	2·57

These two tables bring out the following points:—

(1) The external diameter of the proximal convoluted tubule does not change on activity;

(2) A large lumen is developed in this tubule during diuresis. It varies with the degree of diuresis, and is markedly increased by obstruction of the ureter. Taking the average of all our observations it amounts to nearly 40 per cent. of the total diameter of the tubule;

(3) The distal convoluted tubule is expanded considerably (from 140 to 150 per cent. of its mean at rest); and

(4) The lumen, of considerable size (42·3 per cent. of the total diameter) even in a resting kidney, is more than doubled, and becomes 69·2 per cent. of the total diameter.

We may conclude, then, that the first convoluted tubule, *i.e.* that portion which is subjected to the highest internal pressure, is relatively inextensible transversely. The second convoluted tubule, on the other hand, is transversely extensible. From a further examination of our sections, we judge that the proximal convoluted tubules do indicate an extension in the longitudinal direction, but our present methods do not allow us to state this decisively.* All the results indicate that an internal pressure has existed during diuresis.

Conclusions.

Measurements of the diameters of the various portions of the renal tubule in the cat, when at rest and after diuresis under various conditions, show that Bowman's capsule, the glomerulus, and the second convoluted tubule are extensible structures, and are expanded during diuresis. The glomerulus leaves the capsule wall, a considerable accumulation of secretion being found between them. The lumina of all parts of the tubule become greatly enlarged.

All the appearances found are explained as resulting from the action of a high pressure in the fluid secreted by the glomerular epithelium, and are all in accordance with the propulsor theory of the action of the glomerulus.

* If we may make the assumption that the volume of the cells of the convoluted tubule does not alter during diuresis, then the magnitude of the surface areas of the cells in a transverse section of the tubule gives us an indication of any change in length. If, for this purpose, we examine the results of Experiments 10, 11, 12, and 13, where we have direct comparisons of active with resting kidneys, we find that in all instances the proximal convoluted tubules are markedly stretched longitudinally. In Experiments 10 and 13 there is considerable shortening of the distal convoluted tubules, and in Experiments 11 and 12 slight shortening. In Experiments 10 and 13 the blood-pressure was high and the diuresis good. In Experiments 11 and 12 the blood-pressure was lower and the diuresis only moderate. Hence it would appear that, with a high internal pressure, this portion of the tubule is shortened, *i.e.* tends towards the spherical shape.

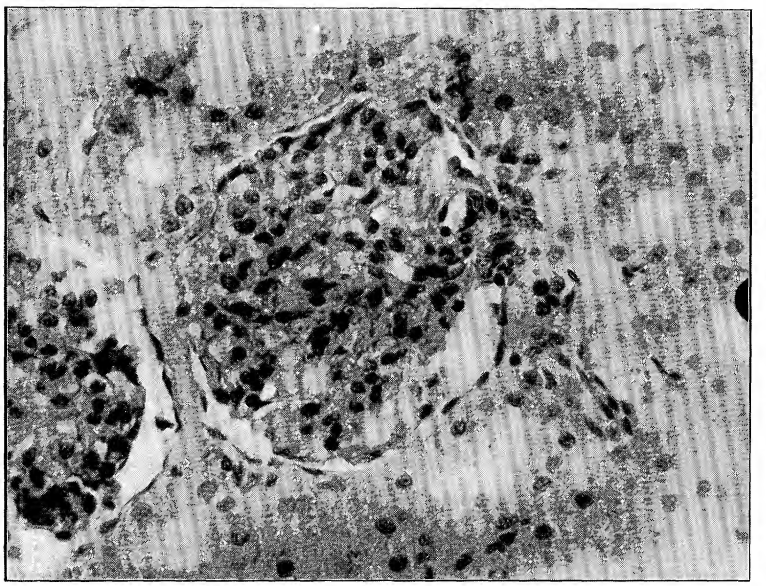

FIG. 1.

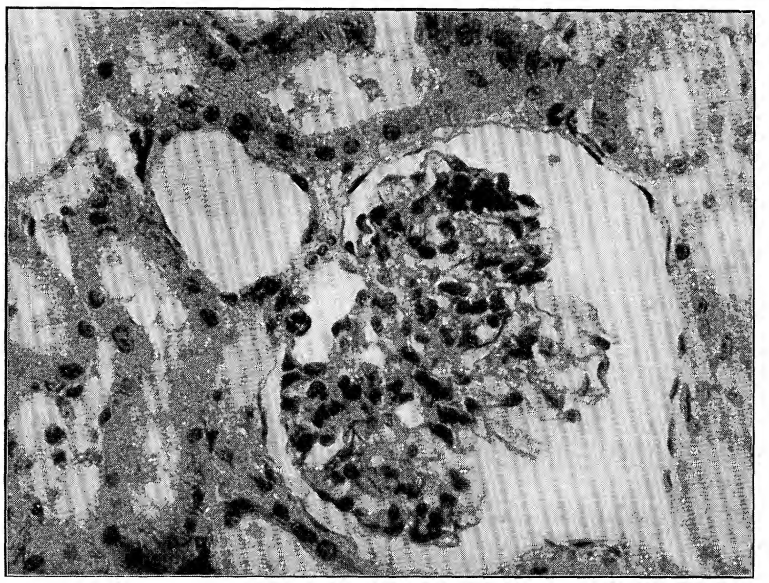

FIG. 2.

FIG. 3.

DESCRIPTION OF PLATE.

Fig. 1.—Microphotograph of Cortex of Dog's Kidney at Rest. ×500.
Fig. 2.—Microphotograph of Cortex of Opposite Kidney after Activity. ×500.
Fig. 3.—Cat's Kidney. Drawing of glomerulus and tubules after activity, showing dilatation of neck of tubule. ×500.

The Controlling Influence of Carbon Dioxide in the Maturation, Dormancy and Germination of Seeds.—Part II.

By FRANKLIN KIDD, B.A., Fellow of St. John's College, Cambridge.

(Communicated by Dr. F. F. Blackman, F.R.S. Received March 25,—Read May 14, 1914.)

CONTENTS.

Introduction.

In the first part of this paper the influence of carbon dioxide in inhibiting the germination of moist seeds was described. The results obtained are summarised on pp. 623–625 of this paper.

In the present paper the relation of this inhibitory effect of carbon dioxide to temperature and oxygen supply is first to be examined, and then will be studied further narcotic or inhibitory effects of CO_2 as

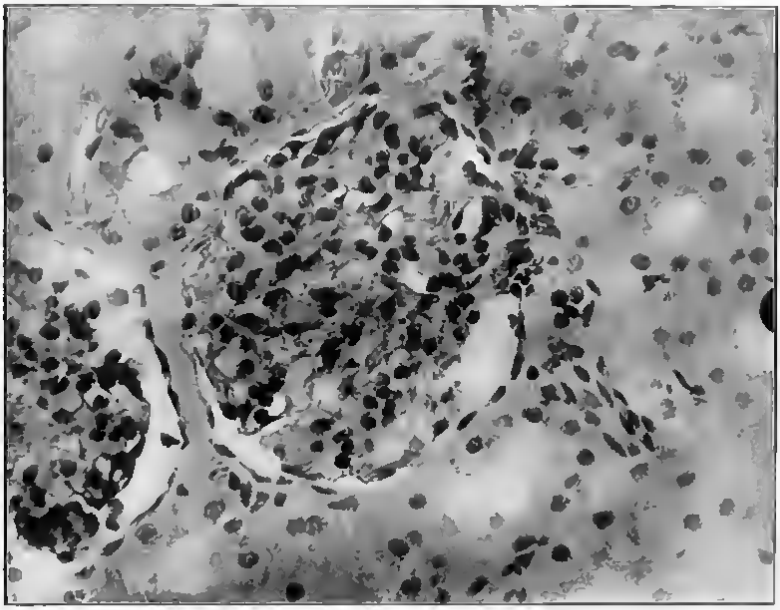

FIG. 1.

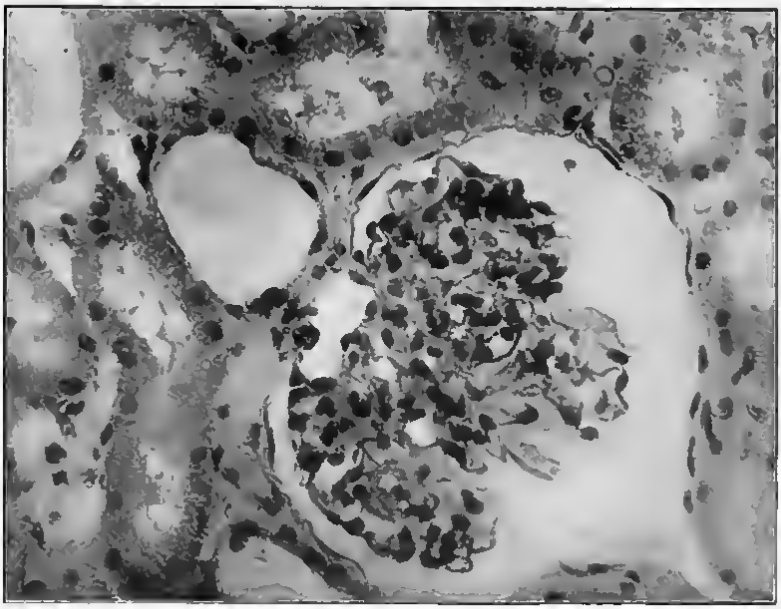

FIG. 2.

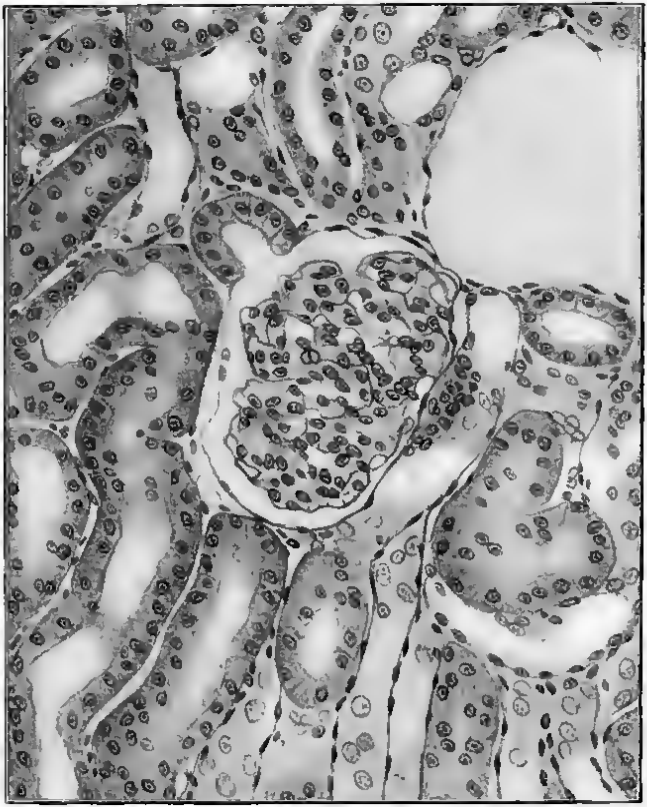

FIG. 3.